Learning and Animal Movement

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Abstract

Integrating diverse concepts from animal behavior, movement ecology, and machine learning, we develop an overview of the ecology of learning and animal movement. Learning-based movement is clearly relevant to ecological problems, but the subject is rooted firmly in psychology, including a distinct terminology. We contrast this psychological origin of learning with the task-oriented perspective on learning that has emerged from the field of artificial intelligence. We review conceptual frameworks that characterize the role of learning in movement, discuss emerging trends, and summarize recent developments in the analysis of movement data. We also discuss the relative advantages of different modeling approaches for exploring the learning-movement interface, including techniques gleaned from the psychological and machine learning fields. We explore in depth how individual and social modalities of learning can matter to the ecology of animal movement, and highlight how diverse kinds of field studies, ranging from translocation efforts to manipulative experiments, can provide critical insight into the learning process in animal movement.

INTRODUCTION

Animal movement takes many forms and is critical to ecological processes. This understanding has given rise to a relatively young but rapidly growing sub-discipline of ecology called movement ecology (Nathan 2008). At the same time, the subject of learning has been studied from the perspective of animal behavior, both in the context of ecological interactions and in the context of movement itself. Animal behavior has a well-established and celebrated history of understanding learning and there has been recent growth in connecting learning and memory to animal movement behavior (e.g., Fagan *et al* . 2013). At the same time, a recent explosion of ideas about learning in artificial intelligence is now reshaping the landscape of learning, and now the lines dividing the functioning of machines and living organisms are starting to blur.

In addition to these recent developments, the ability of ecologists to observe animal movements and behaviors remotely in the wild has been steadily increasing. The collection of massive amounts of data on animal movement patterns, primarily via remote sensing, is now possible at a scale and level of detail previously unimaginable and can be linked with similarly improving remotely sensed or modeled environmental data. Furthermore, more recent advances in bio-logging, including accelerometers, proximity measures, audio- and

video-recording devices, provide direct information on some of the environmental, physiological, and social contexts of movements. This coupling of movement patterns with behavioral, social and environmental contexts has led to novel opportunities to make inferences about possible learning mechanisms and meld ideas from animal behavior, movement ecology, artificial intelligence, and remote sensing in the context of ecology of learning and animal movement. We develop such a synthesis here.

We start with a focus on learning as a means for acquiring information and making decisions. Employing two related definitions of learning, one from psychology and the other from computer science, we evaluate the benefits, costs and limitations of learning in the context of animal movement. Next, we address the modality of learning in animal movement, ranging from individual to social. We then develop links to related disciplines: psychology, animal cognition, and statistical learning. We close with an overview of approaches to studying the process of learning and animal movement, whether from experimental or observational studies, and discuss the role that models can play in this endeavour. Finally, we make some concluding remarks and suggest areas for future developments.

INDIVIDUAL INFORMATION ACQUISITION AND DECISION MAKING

Definition of learning

We start with a *psychology-based definition* of learning, which states that learning is a cognitive response to information acquisition that occurs via an individual's experience that results in a detectable and consistent change in neurophysiology and/or behavior (Box 1). Movement intersects with this definition of learning in several key ways. First, movement will give rise to learning if the movement leads to acquisition of information by introducing an animal to a new environment or state. Second, the learned information can give rise to new movement decisions if the information acquired is used to change movement patterns. Lastly, learning can be about movement itself, for example, when an animal learns where and when to migrate by imitating conspecifics. Figure 1 depicts these connections among movement, information processing, the environment, and the internal states of the animal.

Although researchers can access cellular evidence for neurophysiological changes arising from information acquisition and storage directly via functional magnetic resonance imaging or similar methods (Marsh *et al.* 2010), these approaches are impractical in studies of animals in the wild and most ecologically relevant evidence for learning comes from observing changes in behavior as a result of experience. Thus, although the definition of learning above does not strictly involve decision-making, the ecological implications of learning are often intimately tied to the decision-making process. In movement ecology, researchers deduce that learning has taken place by observing changes in decision making after experiences. Thus, discussions of learning in movement ecology often involve the decision-making process, so learning in the context of movement decisions is more like learning as defined in artificial intelligence: improved performance for a specific task as a result of prior experience. This definition, which we refer to as the *task-based definition* , differs from the psychological definition because it is directly tied to improvements in performance for a specific task based on experience (Box 1).

The learning process

The process of learning includes all the steps needed for information acquisition based on experiences encountered. Broadly, these steps include attention to relevant information, perception of the information, acquisition of that information, finally storage and retrieval (memory) of that information. At this point that the information can be acted upon, for example, to make a movement decision (Figure 1).

Diverse factors may impede or enhance an animal's attention to information from its environment or from other individuals. For example, animals in unfamiliar environments may be more (or less) observant of environmental cues (Wolfe 1969) and certain types of social interaction may increase or decrease attentiveness, leading to social learning (Heyes 1994). Other factors, such as the internal state of an animal (Dorrance & Zentall 2001) or its risk sensitivity (Bacon *et al* . 2010) may also play a role in determining attentiveness (Figure 1).

2

The perception and acquisition of information depend on an animal's sensory capacities. For most animals, certain sensory cues will be easier to detect than others, which can lead to different hierarchies of sensory cues, though that hierarchy may itself be altered contextually. For example, many aural and olfactory cues may be more important than visual information at night (Zollner and Lima 1999). Once acquired, information must be committed to memory as part of the learning process. Storage and retrieval of learned information is essential for decision making, which can be based on recent events or information remembered over long periods of time (Abrahms *et al* . 2019; Polansky *et al* ., 2015).

A test of successful learning is the ability to make a decision using information from past experiences that discriminates among alternative strategies. For example, in laboratory studies, exposure to spatially distributed food rewards in mazes can affect the movement choices of rats (Leonard and McNaughton 1990). Similarly, for wolves, memory-related statistical metrics like 'time since last visit' to a location may form the basis for movement decision discrimination (Schlägel *et al* . 2017). Of course, this link between experiences and decision making is context-dependent, being modulated by layers of complexity regarding habitats, social status, and internal states (Figure 1).

Benefits and Costs of learning

All mobile organisms face a wide variety of spatial challenges that influence individual fitness and present opportunities for decision making shaped by learning. Foraging opportunities and energetic constraints are patchy in space and time, in large part because the underlying physical and biotic processes are also patchy. Optimal foraging theory (Stephens and Krebs 1986; McNamara and Houston 1985; Mangel and Clark 1988) provides a framework for understanding how benefits accrue from foraging in patches that offer the highest returns of energy or nutrient intake per unit time relative to time or energetic costs. Lost opportunities for social interaction, breeding opportunities, reproductive care, or shelter, and the risks of mortality due to predation, parasitism, or disease can then be taken into account.

When the rate of environmental change varies across time and space, as is common along elevation or rainfall gradients, theory suggests an animal may be able to improve its fitness through appropriate patterns of nomadic or migratory movement (e.g., Fryxell & Sinclair 1988). Field studies support this theory. For example, migratory ungulates can choose patches at a landscape scale that yield appreciable improvement in rates of energy gain, even when such gains are transitory and require continual nomadic repositioning (Fryxell *et al.* 2004; Holdo *et al.*2009). Memory can also influence the choice of movement patterns. For example, when undergoing seasonal transitions between ranges, migratory ungulates can obtain fitness benefits by remembering previous trajectories (Bracis & Mueller 2017; Jesmer *et al.* 2018, Merkle *et al* . 2019).

Researchers have investigated how learning can influence and confer advantages to moving organisms. Agent-based models of foragers with and without spatial memory have shown how fitness accrues from moving to acquire reliable information, even when that movement process requires sampling sub-optimal patches (Bracis*et al.* 2015). This is particularly clear when naïve animals are presented with an unfamiliar environment and movement is exploratory. However, even experienced individuals can benefit by spatially sampling a dynamic environment, in particular when resources can be depleted (Boyer & Walsh 2010). In this case, movement keeps current the information needed for appropriate decision making.

Given that foraging often results in resource depletion, fitness may also be improved through informed departure criteria based on marginal value leaving rules (Charnov 1976; Arditi & Dacorogna 1988; Brown 1988). The field of "sampling behavior" (Stephens 1987) extends ideas originally developed within the optimal foraging theory framework, which traditionally assumed that animals are omniscient (Krebs & Inman 1992; Stephens *et al.* 2007b). One sampling framework considers when animals should visit a patch to assess whether it has changed in value (Green 1980), whereas another framework focuses on the value to tracking a changing environment (Shettleworth *et al* . 1988). Foragers that sample patches or track changing conditions are learning about the current state of the environment (Stephens 1987). Informed decision making about which patches to feed in and how long to do so requires reliable expectations regarding resource availability, predation risk, and energetic costs across an individual's home range, as well as the capacity to estimate these

same variables at a given spatial location. For example, primates foraging on fruit track the productivity of different trees and possibly fruit ripeness (Janson & Byrne 2007).

Learning can also help improve fitness even when spatial movement processes are not directly tied to foraging (e.g., territorial defense, migration, reproduction) (Box 2). For example, learning can provide advantages in dominance interactions (Kokko *et al.* 2006), efficiency of movement (Stamps 1995), and effective escape from predators (Brown 2001), all of which can translate into fitness benefits (Brown *et al* . 2008; Patrick & Weimerskirch 2017). For territorial species, learning can influence how conflicts drive pattern formation (Stamps & Krishnan 1999, 2001; Sih & Mateo 2001) and alter strategies for territorial defense (Potts & Lewis 2014; Schlägel & Lewis 2014; Schlägel *et al.*2017) For migratory species, this includes determining least-cost migration corridors between seasonal ranges (Bischof *et al.* 2012; Poor *et al* . 2012).

While learning may have benefits, acquiring information based on experiences encountered does not come without costs. For example, information gathering can require substantial investment in time and/or energy, and may heighten risk (Eliassen*et al.* 2007) or come at the expense of lost opportunities for foraging, social interaction, or search for suitable breeding sites (Dall *et al* . 2005). The machinery for learning can also exact an ongoing energetic cost (Niven 2016).

Limitations to measuring learning from animal movement patterns

Typical methods for recognizing learning in animal movement patterns do not measure the acquisition of information directly but rather rely on the *task-based definition* of learning, which requires improved performance for a specific task, based on acquired experience (Box 1). There are limitations to such methods, and these restrict the utility of uncontrolled field studies where learning. It is a general challenge in the study of wildlife, where context, perception, internal states, and unknown environmental cues all determine an animal's response, to unambiguously explain an observed movement. is discerned from animal movement patterns. For example, the "time since last visit" behavior in wolves, described above, may not require memory. External factors, such as decaying scent marks, could instead be used to keep track of time since last visit(Schlägel & Lewis 2014).

Obvious and obscure alternative explanations to learning and memory must be carefully considered in uncontrolled field studies. Table 1 categorizes a number of movement studies according to the level of evidence for learning – from strong to simply consistent with learning. For each we provide other, non-learning interpretations of the data that cannot be definitively excluded (Table 1).

PATHWAYS OF LEARNING FOR ANIMAL MOVEMENT

Individuals can experience or gain information about their environment via different pathways—individually (i.e., by direct interaction with the environment (Dall*et al.* 2005)) or socially (i.e., by observing others (Bandura & Walters 1963; Rendell *et al.* 2010)), with *learning*demonstrated by a change in an individual's behavior due to its experience (Box 1).

Individual Learning

Much of an animal's individual learning is via an associative mode; that is, an association is made between a stimulus and an outcome. Associative learning may arise either from classical (Pavlovian) conditioning, where an animal associates a biologically relevant stimulus (e.g., food) with a previously irrelevant stimulus (e.g., railway tracks), or from operant (instrumental) conditioning, where the behavior of the animal is controlled by the consequences of that behavior (e.g., feeding on grain on tracks leads to a food reward).

These learning processes can make a behavior more likely through positive reinforcement (via rewards) or negative reinforcement (via unpleasant stimuli), or less likely through punishment or inhibitory learning (again, via unpleasant stimuli). For example, a bear foraging on railway tracks (Murray*et al.* 2017) might be more likely to forage when it receives grain rewards (positive reinforcement) but less likely to forage through negative interactions with moving trains (punishment or inhibitory learning). Additionally, it might increase its level of vigilance through negative interactions with moving trains (negative reinforcement).

4

One associative learning mode relevant to animal movement is discrimination learning, where an animal learns to respond differently to distinct stimuli. For example, because homing pigeons can discriminate between the presence and absence of anomalies in magnetic fields, magnetoreception could be used for navigation (Mora *et al.* 2004).

Two *nonassociative* learning modes that are relevant to movement are habituation (decreased response to a stimulus after repeated exposure) and sensitization (increased response to a stimulus after repeated exposure). These modes are related to the strength of association between stimulus and outcome, rather than the association itself. For example, the sensory responsiveness of honey bees declines after bees are subjected to low sucrose sugar solutions (habituation) and increases after bees are subjected to high sugar solutions (sensitization) (Scheiner 2004). In turn, the sensory responsiveness of honey bees constrains individual foraging plasticity and skews the collective foraging decisions of colonies (Scheiner 2004). Box 1 provides further details on these modes of learning.

Another mode of learning, latent learning, is also relevant to animal movement (Franks *et al.* 2007). Latent learning involves the gathering and storing of information, without immediate reward, such as when animals learn their migration route away from breeding grounds after they are born (e.g., in autumn) and must use that information to migrate back to breeding grounds in the spring.

Social learning

Social learning is an umbrella term for the learning pathway that includes transfer of skills, concepts, rules and strategies that occur in social contexts and can affect individual behavior. Types of social learning include (i) social facilitation (increased probability of performing a behavior in the presence of a conspecific), (ii) local enhancement (an individual's interest in an object or location mediates interest/movement by others), and (iii) imitation (novel copying of a model behavior through observation that results in a reliably similar outcome) (Visalberghi and Fragaszy 1990). Note that these are distinct from the transfer of declarative or procedural information via direct information exchange, such as in bee dancing, to relay information concerning resource locations (Leadbeater & Chittka 2007)

Each type of social learning is relevant to movement ecology. For example, social facilitation explains movement in bison: individuals were more likely to travel to a given new location when in a group where another animal had knowledge of that location (Sigaud *et al.* 2017). Local enhancement also occurs in ants where leaders provide guidance to naïve individuals as to the location of food resources (Franks & Richardson 2006), and in elephants where matriarchs lead herds to waterholes not known to the rest of the group (Fishlock *et al.* 2016). Imitation can be seen in fish, where translocation experiments demonstrate how naïve individuals learn migration routes through association with experienced individuals (Helfman & Schultz 1984), as well as in replacement experiments where the long-term re-use of resting and mating sites can be socially learned rather than selected on the basis of quality (Warner 1988).

Individual learning can interact with social learning. For example, independent exploration allows ants to improve upon the paths they have learned via social learning through tandem running (Franklin and Franks 2012). Here, independent exploration is the basis for improvement of route navigation, which can then be distributed within a colony via 'information cascades.' More generally, individual learning may be modulated by associational acquisition, where the options for individual learning are constrained by the choice of individuals with which an animal associates (Fragaszy & Visalberghi 2004).

Social learning is emphasized though existing social bonds, such as when it manifests vertically from parent to offspring. For example, elephants will learn resource locations in complex landscapes through both vertical and horizontal transmission (Bowell *et al.* 1996) and long-term pairing may enhance transmission between maternal-offspring pairs. For example, paired whales may complete entire migrations together (Hamilton & Cooper 2010), thus enhancing the potential for social learning.

However, social learning does not always confer a net benefit (Giraldeau *et al* . 2002), and may result in costly strategies of movement and resource use (Sigaud *et al.* 2017). For example, tested alone, adult female

guppies that had shoaled with trained conspecifics as they swam to food used the same route used by their trained fellows, even if the route taken by the trained shoal was longer and more energetically costly than were alternative routes (Laland & Williams 1997, Giraldeau *et al* . 2002).

LEARNING AND SPACE USE: CONNECTIONS TO OTHER DISCIPLINES

We distinguish two fundamental constructs for learning in conjunction with animal movement: *updating the world model* and *building a new world model* . To understand the difference between these, it helps to assume that the animal has a cognitive model of the world ($\hat{Q}$) and a set of "policy rules" (β) for mapping conditions, including the snapshot of that cognitive model and the state or priorities of the animal, into outcomes, in particular movement decisions. The policy rules can be thought of as the coefficients of a function governing outcomes in terms of conditions. Within this construct, *updating the world model* refers to the process of movement through a world, acquiring and storing information about the world, updating the world model $\hat{Q}$, and acting upon that knowledge according to the fixed set of policy rules β. The learning process itself is limited to updating the world model. Note that this kind of learning is only meaningful if the world itself is dynamic, with resources or threats moving or depleting and regenerating in a way that makes it beneficial, or even necessary, to update expectations rather than navigate with an essentially fixed map. When confronted with a new world, either via dispersal, translocation, or a significant perturbation to the existing world, the very structure of the world model and the policy rules both need to be adjusted by *building a new world model* . These two fundamental kinds of learning are schematized in Figure 2 where an elk's movement among three dynamic patches constant updating of information (*updating the world model*), a process with relies on moving between those patches. But when a patch is significantly perturbed, or becomes unusable in a novel way, the fundamental structure of the world needs to be altered (*building a new world model*), and novel policy rules to govern interaction with novel elements needs to be developed.

The main distinction between *updating the world model* and *building a new world model* appears in a slightly different form in the machine-learning literature, where the two kinds of learning are labelled as *base-level* and *meta-level.* Specifically, *"The base-level learning problem is the problem of learning functions, just like regular supervised learning. The meta-level learning problem is the problem of learning properties of functions, i.e., learning entire function spaces"* (Thrun and Pratt 1998). The function spaces in our analogy comprise $\hat{Q}$, whereas the learning functions are the coefficients β. In the neurosciences, the terms model-based and model-free reinforcement learning are used in analogy with base-level and meta-level learning (Doll *et al* . 2012).

It is also interesting to note that complex behaviors that appear to involve decision-making can arise from other mechanisms of self-organized behavior. Self-organization occurs when simple rules lead to complex behavior (Gros 2015). A prominent theoretical example is cellular automata whereby a specific rule set, such as "the game of life," gives rise to agent-like configurations that may travel, replicate, and combine. Self-organized robots (Box 3) can exhibit emergent behavior, such as autonomous direction reversal, which an external observer could mistakenly interpret as decision-making (Kubandt *et al* . 2019). Because self-organization is not purposeful, an agent solely based on self-organizational principles will not be able to improve, or to "learn" its score in a given task.

Statistical Learning: Machine Learning Approaches and Beyond

Statistical learning (Hastie *et al* . 2009) is a branch of machine learning concerned with the development and study of algorithms to perform specific tasks with minimal instruction. The tasks involve an explicit goal, such as parameter estimation or classification, and require a clear objective function, such as minimizing a cost function or correctly classifying data. To the extent that animals also have clear objective functions (e.g., ultimately: increasing individual fitness; proximally: eating, avoiding being eaten, reproducing), and that these objectives might be satisfied by performing a specific movement-related task (e.g., selecting appropriate places to forage), it is useful to draw a general analogy between a machine-learning algorithm and an animal that learns. As described above, we use the term*task-based learning* when referring to this type of process.

A wide range of machine learning approaches emphasize the importance of improvement through experience

(Jordan & Mitchell 2015), which is close to some definitions of animal learning. Good examples are artificial neural networks (ANN), a class of biologically inspired learning algorithms. The input of an ANN, typically the sensory perception of the agent or animal, is propagated through a network of idealized neurons, which is readjusted by experience-generated reward signals. The output of the ANN induces observable behaviour.

Another learning-like algorithm is a Bayesian probabilistic model for inference (which can, incidentally, also drive an ANN). While Bayesian reasoning is most often applied for statistical tasks such as parameter estimation and complex model fitting, it is also viewed as a central, probabilistic model for human cognition and learning (Chater *et al.* 2006; Tenenbaum *et al.* 2006). In the specific context of animal movement, prior information represents existing knowledge or existing preference sets (e.g., spatial memory and selection coefficients). Bayesian perspectives readily permit such prior knowledge to be updated with new data (experiences) gained by an animal's movement through the environment. For example, Michelot *et al.* (2019) draw an explicit analogy between stochastic rule-based animal movement and a Gibbs sampler performing Markov chain Monte Carlo sampling. The resulting posterior distributions accurately reflect the animal's resource selection function (RSF). The equivalence between an optimizing algorithm and an animal gaining familiarity with its landscape provides an interesting template. One could generate a similar animal (sampler) that does update its movement coefficients based on the mismatch between its experiences and the environment. Box 3 builds on these rule-based decision-making ideas to draw connections between mobile autonomous robots and learning animals.

Reinforcement learning

Reinforcement learning is a paradigm involving iterated remapping of situations to actions with the goal of maximizing a numerical reward (Sutton & Barto 2017). Learners are not provided rules, but must instead employ repeated trials to discover relationships between actions and rewards. This framework has strong parallels to experience-based frameworks for animal learning. Indeed, a schematic of the reinforcement optimizer for a computer learning to play the game Go is broadly similar to schematics of animal behavior and learning (Table 2). In both frameworks, an agent takes actions (movements) in the environment, and the outcomes of those actions are processed by an interpreter (cognitive model), which either "rewards" or "punishes" the agent, thereby modifying its internal state and modifying its subsequent actions. Additional aspects of realism are that rewards can be short term or delayed, and that the appropriateness of actions is not provided initially but must be learned via exploration.

Criteria of machine learning applied to animal learning

The machine learning literature provides concrete criteria for identifying if an algorithm has learned (Thrun & Pratt 1998). Specifically, given (1) a *task* , (2) *training experience* , and (3) a *performance measure* , if performance at the task improves with experience, the algorithm is said to have learned. This is a useful framework for interpreting observational animal movement data. For example, for the sheep and moose in Jesmer *et al.* (2018) the *task* was maximizing energy intake and the *training experience* was several years of moving around the landscape. The *performance measure* was the question: Did the animals adopt a migratory movement strategy to track variability in energy availability across space and time? Because of an increase in the proportion of migrants in the population over time (and, thereby, an increase in the proportion of individuals with increased energy intake), the animals likely had "learned".

A major challenge to applying machine learning criteria to moving animals involves identifying the *task* and *performance measure* in meaningful ways, given the animals' spatial context and scale of movement. Survival and reproduction are the ultimate tasks, but foraging, resting, finding a mate, and avoiding predation are all proximal tasks. Nonetheless, the framework helpfully and unambiguously associates movement in the environment with *training experience* . Table 2 cross-references a machine-learning example with field studies that provided experimental evidence of learning.

Cognitive ecologists typically have more stringent criteria for identifying learning. For example, experimentation plus control conditions sufficient to rule out alternate explanations are fundamental to confirming the existence of social learning (Reader & Biro 2010). In this framework, experimentation could involve mani-

pulation of physical aspects of the environment, individual animals via translocations or similar means, or the routes governing social transmission of information.

A particularly difficult challenge involves applying the statistical learning criteria to problems where the learning involves *updating the world model* (as described above) in a familiar landscape rather than learning about a fundamentally novel landscape. For example, in the foraging models of Bracis *et al.* (2015, 2018), the task is maximization of instantaneous energy intake, the training *experience* is the movement (together with the acquisition of information for updating the cognitive map), and the *performance measure* is the amount of forage obtained. However, because the modeled movement process is stationary (in the stochastic sense, meaning that the underlying movement parameters do not change over time), there is no measurable improvement over the long term, merely a constant updating. Nevertheless, without learning (i.e., without the ability to update the cognitive map), the forager performs much worse. Exploring these theoretical discoveries in field systems appears quite challenging because it is difficult to experimentally manipulate the map updating. This contrasts with the heightened feasibility of experimental studies in which learning can be assessed as improvement in animals' performance as a function of time (see below; Fig. 3).

LEARNING ABOUT LEARNING: METHODS AND APPROACHES

Experimental vs. observational frameworks for gathering evidence of learning in movement

The connection between learning and animal movement has been inferred from studies that range from classic experiments to pure observational data. These diverse data types provide distinct insights into how movement can be used to infer learning processes.

Experimental Studies

Informative experimental studies of learning and movement derive from both field and laboratory settings (Jacobs & Menzel 2014). For example, experimental resource manipulations demonstrate that hummingbirds can learn abstract concepts like spatial position (Henderson *et al.* 2006) and can encode spatial location on the basis of surrounding landmarks (Flores-Abreu *et al.* 2012). In another field system, Preisler *et al* . (2006) tracked elk movements in relation to experimental treatments involving all-terrain vehicles (ATV) driven through a landscape. They found that the probability of elk responding to ATVs was much higher when the animal was on an ATV route, even if the ATV was far away. These data suggest that these animals have learned to associate ATV presence with their routes.

In laboratory settings, radial mazes and water mazes (e.g., Leonard and McNaughton 1990) have been widely used to study how quickly rodents can learn movement routes and improve their efficiency. Other kinds of laboratory arenas built for insects, have demonstrated for example that pesticide exposure can impair spatial learning of the distribution of resources in bumblebees (Stanley *et al.* 2015).

Sometimes field and laboratory experiments can be combined with great benefit, including comparisons among three classic model systems (homing pigeons, bees, and rats; (Jacobs & Menzel 2014)). For example, experimental lesioning studies of young homing pigeons, followed by release in unfamiliar areas, demonstrate that immature birds are very good at learning movement routes and that there is a consolidation phase during which experiences (e.g., encounters with landmarks) are neurally encoded (Bingman *et al.* 2005).

Observational studies

To assess learning from an observational perspective, we must analyze how an animal behaves at a given time based on local conditions and past experiences. In practice observational studies typically record the location of animals and thus their experiences over relatively long time-frames (e.g., multiple years, or entire lifetime). Remotely sensed geographic and climatological data then provide the local conditions the animal is experiencing during movement. Additional information on the behavioral and physiological states of the animal may also be relevant. Fortunately, the ongoing evolution in remote animal tracking and sensing technology means that we are increasingly able to measure physiological and behavioural states over long periods of time (Kays *et al* . 2015).

Data on repeated movement patterns can help us differentiate between hypotheses about learning. For example, data on repeated migration routes has been used to determine whether animals follow resource gradients, rely on memory to navigate, or learn from experience to shape their movement decisions (Mueller *et al* . 2013, Merkle *et a* l. 2019). However, long-term tracking data may also be sufficient for analysis. For example, long-term data tracking the movement of wolves has been use to determine whether animals only follow resource levels, or also rely on the memory of time since last visit to a location (Schlägel *et al.* 2017). Augmenting tracking data with direct data on the information that the animals might gather, for example the location of kill sites (Gurarie *et al* . 2011) or profitable forage patches (Merkle *et al* . 2014), can further enhance our understanding of how animals monitor their environment through time (Gurarie *et al.* 2011).

Comparative studies can be useful for identifying instances of learning. For example, comparing the movement efficiency of juveniles and adults shows that seabirds start by exploring their landscape and then learn to identify the good foraging areas and cues as adults (de Grissac *et al.* 2017; Votier *et al.* 2017; Grecian *et al.* 2018; Wakefield *et al.* 2019). Effects of early-life experience can also be identified by analyzing the site fidelity of animals to their breeding ground (Weinrich 1998) and by comparing the migration patterns of offspring to those of their mother's (Colbeck *et al.* 2013). Finally, comparing the movement of cultural groups, especially if sympatric, can help to assess the effect of culturally transmitted information on animals' use of space (Kendal *et al.* 2018; Owen *et al.* 2019).

Translocations and Reintroductions

Some management actions involve human-aided displacements of animals, either from captivity (reintroductions) or from other wild populations (translocations). Tracking the animals released in such manipulations can provide unique opportunities to understand how the animals adapt to their new environments (He *et al.* 2019). For example, recurring short displacements (such as when animals are repeatedly taken to the same sampling station for physiological samples), can be used to assess how quickly the animal learns the return route to its home range (Biro *et al* . 2007).

Translocations of animals into existing populations can aid understanding of learning when movement behaviors of individuals new to the environment can be compared to those of already-resident individuals. For example, quantifying the rate of convergence of movement metrics between new arrivals and residents could help estimate learning rates. In addition, if translocated animals are sourced from areas that differ in predation risk (or other factors) but released in a common space, comparison of the survival and movement patterns could be useful to understanding how previous experience shapes learning (Frair *et al.* 2007). Translocations of social animals may also create opportunities for newly arrived individuals to learn from resident conspecifics (Dolev *et al.* 2002).

Overall, tracking the movements of animals in novel environments over years or even generations in comparison to historical populations can reveal the importance of learning and cultural transmission and identify the rate at which animals gain knowledge of their environment. For example, Jesmer *et al* . (2018) found that it took multiple decades for translocated bighorn sheep and moose to regain the capacity to identify and follow the optimal forage gradients that existed in their landscapes as they migrated. Likewise, tracking the movement of prey species before and after the introduction of predators into a landscape affords unique opportunities for investigating how animals learn to avoid predators (Ford *et al* . 2015).

Uncontrolled Experiments

Beyond intentional displacements, other management actions can serve as uncontrolled experiments for learning. For example, aversive conditioning is routinely used in wildlife conflict management and could provide guidance on the mode of learning of animals (Bejder *et al.* 2009) and may provide data on the efficacy of different deterrence systems that vary in intensity and/or frequency. For example, Ronconi & Cassady St. Clair (2006) showed that presence-activated deterrent systems were more useful than were randomly activated systems for limiting the landing of waterfowl on tailing ponds from oil extraction. Likewise, fences involving bee hives were more likely to turn away elephants than were bush fences (King *et al.* 2011) and problem elk repeatedly chased by humans and dogs stayed further from town (Kloppers *et al.* 2005).

9

Rapid changes in habitat can also serve as uncontrolled experiments. For example, because ungulates will select areas recently affected by fires (Allred et al. 2011), monitoring the movement of animals in fire-prone systems could help understand how these animals learn about and navigate to novel habitats. Studying movement in the vicinity of new obstacles (e.g., pipelines and roads) and passageways (e.g., road-crossing structures) could help to understand how animals change their spatial patterns as they learn to circumvent these barriers and make use of new structures (McDonald & Cassady St Clair 2004, Ford and Clevenger 2018).

Identifying and characterizing learning

Analytical and computational tools have a special role to play in the context of learning and animal movement. They can be used both to develop new theory, and in the process of inference regarding actual movement behaviours.

Modeling frameworks for exploring how learning operates

Dynamical systems models are often used to investigate learning and animal movement in a purely theoretical context. The most common purpose is to investigate possible emergent patterns, which arise from the inclusion of learning in movement models. Here spatial location and spatial memory are given by variables that change in time and space, and dynamical rules postulate how these variables could change through the interplay of movement and learning. The actual form of the dynamical systems ranges from difference equations used to analyze home ranges (Van Moorter *et al.* 2009), to partial differential equations used to analyse searching ability (Berbert & Lewis 2018) stochastic processes used to investigate patrolling ability (Schlägel & Lewis 2014). Agent-based simulations have also been used to track the development of complex spatial movement behaviours via learning (Tang & Bennett 2010; Avgar *et al.* 2013). Theoretical studies can investigate relationships or feedbacks between movement and learning that generate patterns similar those seen in nature. They can also be used to explore the features of environments where the ability to learn, access and adapt spatial memory might confer benefits. Theoretical explorations are particularly useful for studying the *updating the world model* type of learning, where it is more difficult to make a clear distinction between precipitating events of experiences and movement outcomes.

Machine learning and artificial intelligence are emerging as a powerful paradigm for the analysis of many biological systems. In the context of learning and animal movement, these approaches can map environmental conditions to movement behaviour outcomes without necessarily investigating the learning process itself. An example of such a link is given by Mueller et al. (2011), who employed neural nets to link canonical classes of spatial movement behaviours in ungulates (e.g., nomadism, migration, range residency) to classes of environmental conditions (spatially constant versus variable and temporally constant versus variable). Furthermore, as described earlier, machine learning and artificial intelligence can serve as prototype models for the process of animal learning itself.

Testing for change over time in key movement metrics

Across diverse data types, a key indicator of learning is a change in the response measured as a function of 'time in the environment' (Fig. 3). While not sufficient to say confidently that learning has occurred, a strong signal that an animal's movement behavior has changed with experience suggests that it is learning. For example, the range occupied by a group of newly translocated animals would be expected stay very close to their point of release as they focus on learning attributes of their new environment, but wander more widely as time since release increases as they start to exploit their new environment more widely (e.g., total daily displacement, He *et al.* 2019).

Decreases in the rate of range expansion over time indicates that translocated individuals may have learned to favor certain parts of the landscape. In this case, exploration shifts to an exploitation phase (Berger-Tal *et al* . 2014) as translocated animals exhibit a greater probability of revisiting previously visited areas (Fig. 3a). Similarly, exposure to a hostile landscape element (e.g., human habitation) may condition wild animals to avoid such elements, altering their spatial distribution to favor locations far from habitation (Fig. 3b).

This issue has been particularly well investigated with elephants (Hoare *et al* . 1999, Cheptou *et al* . 2017)

Animals that 'sample' different landscapes during exploratory movements may ultimately settle in landscapes featuring the kinds of elements they encountered and exploited during the exploration phase. This can occur during dispersal, during which animals effectively sample and make decisions in an environment about which they are completely naïve. Wolves have been shown to show less avoidance of human elements, in particular relatively little-used forest roads, in new territories after a greater level of exposure and use during a dispersal phase, suggesting that they might have learned that that benefits of using those human elements outweigh the risks (Barry *et al.* In Press). Translocation, which can be considered an artificial and more abrupt dispersal, also requires decision making in novel environments. Changes in movement behavior (and improved survival) were recorded following translocation of naïve elk from a savannah landscape in Alberta to a forested landscape in eastern Canada (Fryxell *et al* . 2008).

Migration is another scenario featuring time-dependence in characteristics of movement (Fig. 3b). For example, both Mueller*et al.* (2013) and Jesmer *et al.* (2018) report changes in migration performance as a function of animals' time in a landscape (Table 2). On smaller scales, foraging journeys from a central place and other kinds of daily activity patterns can show the same kind of performance gains as a function of experience or age (de Grissac*et al.* 2017; Votier *et al.* 2017; Wakefield *et al.*2019) (Table 1).

Statistical inference to identify learning in movement processes

Analytical and computational tools may also be used to infer learning processes from data. For example, the step-selection function (SSF, (Fortin*et al.* 2005) is of particular utility when it is connected to regular samples of location data and allows for inference of movement parameters that depend on different habitat types. Computationally efficient approaches such as integrated step selection analysis (iSSA) (Avgar*et al.* 2016), provide practitioners a straightforward way to evaluate movement decisions against actual observations. A generalized form of the SSF, termed the coupled SSF (Potts *et al.* 2014), allows for the inclusion of memory and past social interactions. Here memory and past interactions can be included into the model, as one or more spatio-temporal maps, sometimes referred to as cognitive maps. Although superficially similar to a changing habitat layer, the contents of the cognitive maps are particular to each individual as they are populated by information gleaned from the individual's past experiences (Fagan *et al.* 2013). With this structure in place in a SSF model, one can test how the individual's movement behavior is governed by maps whose contents arise from different types of memories or social interactions. Coupled SSFs have been used to test for evidence of memory (Schlägel*et al.* 2017) and learning (Merkle*et al.* 2014) in animal movement patterns.

Analysis via SSF assumes that animals' location data are known without error. If error is significant, as it can be for marine systems, a different class of model, known as state space models, are needed. State space models are hierarchical and feature separate models for the movement process and the measurement error process. These models can be modified to include a hidden Markov process, whose latent state is determined by physiological status (e.g., searching or travelling) or by learning (Avgar*et al.* 2016). Such models, while flexible, may suffer from parameter estimability issues (Auger-Méthé*et al.* 2016) and must be implemented with care.

CONCLUSIONS AND NEW HORIZONS

Traditionally, studies of animal learning and movement have taken place in controlled laboratory environments or small-scale field studies. Thanks to animal tracking technologies, increasingly detailed observations of how free-ranging animals move and interact are possible leading to opportunities to formulate and test new ideas about learning and movement. However, potential pitfalls accompany this exciting development. Alternative explanations to learning must be considered, and if these alternatives cannot be ruled out, then we can only infer that observations are consistent with learning (Table 2).

There are two possible approaches to solving this problem. First, field observations can be transformed into controlled experiments via manipulations, as in the hummingbird example in Table 2. While allowing for

incisive analysis, this approach limits the scientific questions to those where such experiments can be set up. A second possible solution is to collect more direct data on the individual experiences over a life-time, including the environmental features of locations animals visit, physiological measurements, and sensory data as made possible by daylight sensors and collar cameras.

Exciting approaches to studying learning and animal movement arise from "uncontrolled" experiments, specifically translocations, reintroductions, aversive conditioning and rapid environmental change. Understanding learning in the context of relocations and environmental change may ultimately help with understanding how animals can adapt to an increasingly complex world, driven by elevated levels of anthropogenic impact from environmental change, habitat degradation, and habitat fragmentation.

The emergence of machine learning as a dominant paradigm for solving human problems provides fertile ground for modeling and understanding learning from animal movement patterns. Here, processes such as reinforcement learning have close natural ties to animals learning to move so as to maximize fitness (e.g., optimal foraging). As machine learning algorithms are currently improving and evolving, we expect this field to shed light on further possible models for learning and animal movement.

Overall, the subject of learning and animal movement is at a crucial point in development and a host of new possibilities are on the horizon. Our goal in this review has been to set the context for these new possibilities and point out some future directions.

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Box 1: Definitions of terms associated with learning

This box defines terms central to a synthesis of concepts from animal behavior, ecology, psychology, and certain quantitative methods.

Foundational Concepts

Learning:

Psychology-based definition: the cause-effect process leading to information acquisition that occurs as a result of an individual's experience.

Task-based definition: improved performance for a specific task, based on experience.

Memory: The outcome (encoding) of learning, i.e., the storage and retention of information over time.

Spatial memory: The memory for where objects/resources/places are in space. Representation of space. Encodes spatial relationships or configurations.

Supervised machine learning : The process by which the machine is trained to perform a task where some input data is already tagged with the correct output. It can be compared to learning in the presence of a supervisor or teacher.

Statistical learning theory : An unsupervised framework for machine learning that deals with the problem of extracting statistical relevant correlations from data.

Modes of Learning

Associative learning: When an animal makes an association between a stimulus and an outcome. Two forms are:

Classical (Pavlovian) conditioning: an animal associates a biologically relevant stimulus (e.g., food) with a previously irrelevant stimulus. For example, a dog presented the sound of a bell rung alongside the presentation of food, will come to salivate at the sound of the bell in the absence of food. Another example would be that a raccoon learns that garbage cans contain food.

Operant (instrumental) conditioning : the behavior of an animal is controlled by the consequences of that behavior. Typically, this behavior develops through sequential reinforcement (e.g., a raccoon learns how to open the garbage can to get food and is rewarded).

Positive reinforcement: Behavior is rewarded and then increases.

Negative reinforcement : Behavior is increased through avoidance of an unpleasant stimulus. (Also known as instrumental conditioning.)

Punishment or Inhibitory learning: Behavior is decreased through avoidance of an unpleasant stimulus. This contrasts with negative reinforcement, where the behavior increases.

Reinforcement learning: *From machine learning:* The learner is not told which actions to take, but instead must discover which actions yield the most reward by trying them. This is synonymous with *trial and error learning* . As in optimal foraging in ecology, the focus is on the balance between exploration (of unfamiliar objects/places) and exploitation (of current knowledge).

Habituation: after repeated exposure, an animal decreasingly responds to a stimulus. The stable end state is the animal's level of tolerance of a stimulus and the outcome is higher tolerance.

Sensitization: after repeated exposure, an animal increasingly responds to a stimulus. The stable end state is the animal's level of tolerance of a stimulus, and the outcome is decreased tolerance.

Pathways of Learning

Social learning: Also called 'transmission', this is an umbrella term that includes includes transfer of skills, concepts, rules and strategies that occur in social contexts and can affect individual behavior. These include:

Social facilitation: An animal has an increased probability of performing a behavior in the presence of a conspecific.

Local enhancement : An individual's interest in an object or location is mediated by the interest or movement of others.

Imitation : Novel copying of a model behavior through observation that results in a reliably similar outcome.

Cultural transmission: Social transmission leading to the development of traditions that are passed down from generation to generation.

Vertical versus horizontal learning: Sometimes referred to as parent versus peer learning, this dichotomy characterizes the generational source of social information.

Information center: Particular locations or events that provide opportunity for information exchange. For example, a community roost may enable individuals to follow well-fed peers to new foraging locations.

Direct information exchange: An animal is provided sender-based, actively communicated information by another individual. For example, honeybees tell their sisters the locations of rewarding flowers.

Optimization-related Terms

Genetic algorithm: A population of candidate solutions to an optimization problem that evolve towards better solutions.

Policy: In machine learning, the mapping of states to actions (e.g., a hungry animal begins to hunt).

Utility function: In machine learning, the assignment of weights or values to agent states. Actions are selected by comparing the values of the predicted states that derive from particular action. For example, a policy involving search versus sit-and-wait strategies will yield different outcomes for a hungry animal.

Adaptive movement: When animals modify their movement in response to a change. In models, adaptive implies movement behaviors that confer fitness/performance benefits.

Box 2: Learning and Movement Processes

Movement is the spatial consequence of a number of different behaviors by animals. For example, a predator searching for predictable but mobile prey must change its location in space to increase the chances it will encounter a prey item. In many situations (e.g., predictable environments or regularly available prey), learning can reduce uncertainty and increase success in such spatial behaviors. We outline a selection of these below:

Search and attack in predation – When prey live in a complex and heterogeneous environment, predators may benefit by adjusting their search and attack behavior over time (Stephens *et al.* 2007a). When predators detect their prey through visual, auditory, or olfactory cues, they can use associative learning to refine their 'search image' and improve their ability to detect and attack prey (Ishii & Shimada 2010). For instance, desert ants (*Cataglyphis fortis*) use associative learning to connect specific odors to food, and then use this food-odor memory to assist their next foraging journey (Huber and Knaden 2018).

Escape from a predator – Spending time in familiar space allows animals to learn motor programs that enhance efficient movement within that space (Stamps 1995). For instance, in response to a pursuing human, Eastern Chipmunks (*Tamias striatus*) within their home range (i.e., familiar space) take half as much time and travel half as far to reach a refuge compared to when outside their home range (Clarke et al. 1993)

Foraging bouts – An animal's rate of energy gain while foraging can increase by collecting information about the environment (Stephens & Krebs 1987), given the environment changes in a (at least somewhat) predictive way. In most of these cases, animals use associative learning to connect the reward of a food source with some aspect (e.g., color, nearby landmark) of that food source. For instance, Rufous Hummingbirds learned the location of flowers that they had emptied in a foraging trial, and in subsequent trials did not waste time visiting them again (Healy & Hurly 1995).

Navigation and migration – Migratory movements notably occur at spatial scales that greatly exceed perceptual abilities of animals (mammals: (Teitelbaum *et al.* 2015); birds: (Alerstam *et al.* 2003). Thus, it is expected that animal migration is based on memory of past experience, and thus learning is likely used to improve migratory performance. For instance, social learning of migration helps ungulates improve energy gain (Jesmer *et al.* 2018) and helps birds reduce costs (Mueller *et al.* 2013).

Home range or territory selection – The decision process of choosing the size and location of home range or territories can be thought of as a learning process of integrating new information about the distribution of resources of a landscape (Mitchell & Powell 2004). For instance, home range size is often smaller in areas with fewer resources available (e.g., (Morellet *et al.* 2013; Viana *et al.* 2018). Further, increased exploration events, presumably to sample new locations when others are unavailable, can result in larger home ranges (Merkle *et al.* 2015).

Box 3. Robotics: Learning by Mobile Autonomous Agents

Robots that move and act autonomously, learning as they go, are confronted with tasks that parallel, in some ways, the life needs faced by moving animals. As in living animals, future decisions by a mobile autonomous robot hinge on what the learning robot experiences and encounters. Consequently, it is interesting to investigate how animal decision making about movement (Fig. 1) may be understood using concepts commonly used in robotics and control theory (Jordan & Mitchell 2015).

The basic model of an autonomous learner includes the following ingredients:

1. The external *environment.*
2. An internal *state representation* (sometimes termed a *world representation*).
3. A set of possible *actions.*
4. A *policy map* that relates *state representations* to *actions.*
5. *Information acquisition,* which is a consequence of *actions* interacting with the *environment* and the *state representations.*
6. *Value functions that quantify benefits and consequence of actions as represented by the internal states.*

A robot's *state representation* simplifies all the information in the environment to a manageable (pruned and stylized) subset of relevant information that can eventually be linked to *actions* . Unsupervised *state representations* (Lesort *et al.* 2018) in which there are no performance measures, may be particularly relevant as constructs for how learning operates in animals. *State representations* allow the *policy map* to act on a dimensionally reduced decision space (the collection of states), which dramatically simplifies the task of learning individual policies.

A *policy map* structures the relationship of the robot's *state representation* to possible *actions* . A *policy map* may be complete, mapping all possible states to actions, or calculated on the run. Monte Carlo tree search, as used in the Go program AlphaGo from Google Deepmind (Silver *et al.* 2017), determines the next move via an extensive stochastic search. As an additional complication, a robot may possess several *policy maps* and then select among the alternatives in a rule-based fashion.

Specified in this way, the basic details of a mobile autonomous robot map quite closely onto a formal conceptualization of the learning process in the context of animal movement (Fig. 1).

Table 1: Case Studies of Learning and Animal Movement

Reference	Species	Spatial Processes Involved	Individual Learning vs. Social Learning	Learning in Novel or Familiar Contexts ?	Learning Linked to Memory ?	Simple Elapsed Time ?	Juvenile vs. Adult Comparison ?
Barry *et al.* in review	Wolves	Natal dispersal Territory formation	Individual	Novel	Y	Y	N
de Grissac *et al.* 2017	Wandering Albatross	Foraging	Individual	Novel	N	Y	Y
Grecian *et al.* 2018	Gannets	Foraging Exploration	Elements of Both	Novel	Y	N	Y
Leadbeater & Chittka 2009	Bumblebees	Foraging	Social	Novel	N	Y	N
Lihoreau *et al.* 2012	Bumblebees	Foraging	Individual	Familiar	Y	Y	N
Papastamatiou *et al.* 2011	Sharks	Orientation Patch use	Individual	Familiar	Y	N	Partly
Scott *et al.* 2014	Sea turtles	Foraging Migration	Individual	Novel	Y	Y	Partly
Sigaud *et al.* 2017	Bison	Foraging Patch Use	Social	Novel	Y	Y	N
Teitelbaum *et al.* 2016	Whooping Cranes	Migration Shortstopping	Elements of Both	Familiar	Y	Y	Y

23

Reference	Species	Spatial Processes Involved	Individual Learning vs. Social Learning	Learning in Novel or Familiar Contexts ?	Learning Linked to Memory ?	Simple Elapsed Time ?	Juvenile vs. Adult Comparison ?
Votier *et al.* 2017	Gannets	Foraging Exploration	Elements of Both	Novel	Y	Y	Y

	Machine Learning Example	Empirical Examples	Empirical Examples	Empirical Examples	Empirical Examples
Step	**AlphaGo Zero** Silver *et al.* 2017	**Hummingbird Traplining** Tello-Ramos *et al.* 2015	**Crane Migration** Mueller *et al.* 2013	**Experimental Elk Translocation** (Frair *et al.* 2007)	**Sheep and Moose Migration** Jesmer *et al.* 2018
Task	Win	Forage efficiently	Migrate efficiently	Exploit environment optimally	Exploit environment optimally
Experience	Repeated play against self	Movement within a controlled array of feeders	Repeated migration journeys across years	Movement away from initial capture/release location	Movement and population persistence over decades
Performance measure	Victories	Path distance per bout	Deviations from straight-line migratory path	Settlement and survival rate	Proportion of green wave exploited Percent of population migrating
Demonstrated improvement over time (or in comparison to benchmark)	Increased competitive ranking	Decreased length of movement path	Decreased length of migratory journey	Increased rate of residency	Increased migratory tracking and universal migration
Plausible learning mechanisms	Reinforcement learning	Positive reinforcement	Spatial memory Social learning Positive reinforcement	Positive reinforcement (forage) Negative reinforcement (predation) Horizontal social transmission	Vertical transmission Positive reinforcement (individual moose foraging) Positive reinforcement (social sheep foraging) Cultural transmission

	Machine Learning Example	Empirical Examples	Empirical Examples	Empirical Examples	Empirical Examples
Alternative explanations	Not necessary	Controlled experiment	Tested and rejected wind-mediated movement and ontogeny	Mortality-mediated natural selection	Mortality-mediated natural selection Population growth and expansion Kinesis
Evidence of learning?	Yes	Yes	Yes	Consistent with learning but not direct evidence. Population-level rather than individual-level metrics impede direct evidence for learning.	Consistent with learning but not direct evidence. Population-level rather than individual-level metrics impede direct evidence for learning.

Table 2. Mapping Empirical Examples of Learning to Machine Learning Concepts

Table 3: Models for Learning and Animal Movement

Step	Bracis *et al.* 2015	Merkle *et al.* 2017	Avgar *et al.* 2016	Schlägel *et al.* 2017
Task	Maximize consumption Reduce predation	Forage efficiently	Forage efficiently and survive	Patrol
Experience	Movement	Movement among patches	Movement	Movement
Model prediction	Consumption and predator encounter rate	Patch selection	Redistribution kernel	Entire movement path
Null model	Context-dependent behavioural switching	Connectivity, size, and quality of patch	Forage quality, predation risk, competitors, and snow	Movement in response to prey density Distance to territory boundary
Information updated	Location and quality of forage and encounters	Location and quality of patches Memory of past patch quality	Location and quality of habitat	Time since last visit to territorial locations
Improvement via learning	Learning forager outperforms null model	Learning forager is more efficient	Yes	Yes
Plausible connections to fitness	Foraging efficiency Reducing encounters with predators	Past experience leads to foraging in higher quality patches	Past experience leads to better habitat use	Territorial maintenance and defense

25

Step	Bracis *et al.* 2015	Merkle *et al.* 2017	Avgar *et al.* 2016	Schlägel *et al.* 2017
Plausible learning mechanism	Sampling and trial-and-error plus reinforcement	Positive reinforcement	Positive reinforcement	Positive reinforcement

Figure 1. A conceptualization of learning in the context of animal movement. The information gathering pathway appears inside the animal's brain. Note that an individuals' internal state and its environment can influence both the onset of information gathering and how well memory maps onto movement decisions.

Figure 2: A schematic representation of a forager's movement rules in a heterogeneous landscape, how a stable set of rules might be applied, and how landscape disturbance could force an update to the movement rules via learning. In a pre-disturbance world (left three columns), the forager (denoted by the white elk symbol) occupies a landscape with three depletable and renewable resource patches and a water body. The 'real world' is represented in the top row, with all of its complexity. The second row represents the forager's model of that world, which distills the complexity to the most relevant information. Shapes indicate different landscape elements, while colors reflect a quantitative score: darker greens are regenerated, paler greens are depleted. The forager has two movement rules in this landscape (bottom row): 1) move from depleted resource patch to a regenerated resource patch and 2) avoid the water body. The pre-disturbance movements rely on a dynamically updated spatial memory, as the forager learns about a changing environment. Post-disturbance, the forager's world model changes after it gains information about the loss of a potential foraging area, e.g. a new oil well destroys one of the patches. Accordingly, the forager's world model is refined to include a novel categorical element (orange triangle), with its own avoidance rule for movement (dynamic learning).
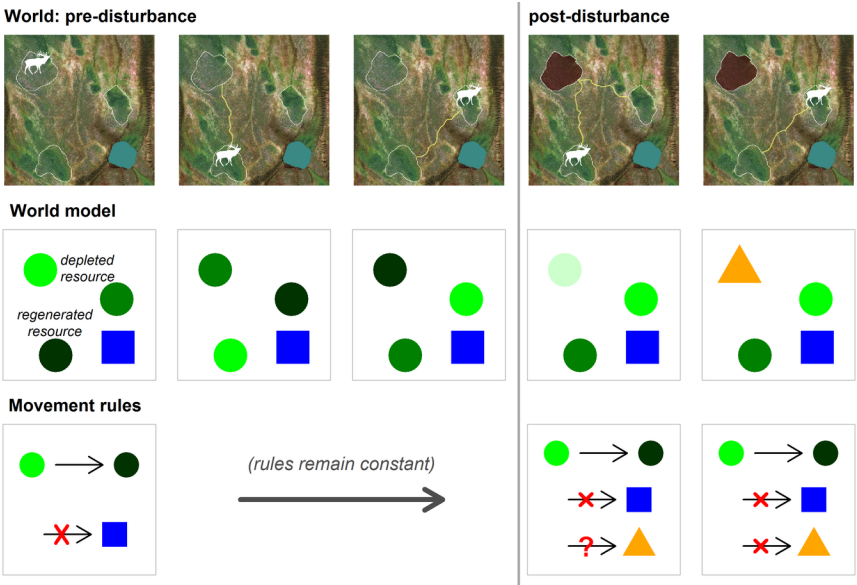

Figure 3: Exemplar movement patterns associated with learning. We represent clusters of movement activity as squiggles and range displacement events as periods of directed motion. In each of the three examples, the process of learning alters the pattern of movement in a statistically detectable manner. Exploration becomes exploitation through repeated visitation (top row). Conditioned responses to habitat elements may manifest as before / after displacement events (middle row). Information gathering during a juvenile (or otherwise

naïve) phase may yield improved efficiency of travel. In all three examples, one or more key metrics will exhibit time-dependence (right column).